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ORIENTATION OF *TALITRUS SALTATOR* MONTAGU (CRUSTACEA AMPHIPODA) IN FRESH, SEA AND DILUTED SEA WATER

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Most of the data regarding the solar or lunar orientation of littoral amphipods refer to their behaviour in dry conditions, both in nature and the laboratory. Only occasionally has their capacity for astronomic orientation been tested in water or on a damp substratum. PARDI & PAPI (1953) immersed *Talitrus saltator* Montagu in sea water and found that it oriented towards the shoreline. Specimens immersed by TERRACINI-DE BENEDETTI (1963) in fresh water fled towards the sea, as did other specimens of the same population when dehydrated and placed on a dry substratum. While a watery medium is capable of provoking a flight reaction, the direction of flight is apparently determined by the salinity. The seaward orientation of animals immersed in fresh water was plausibly attributed to a survival instinct.

The present research aims at verifying the directional tendencies of *Talitrus* when immersed in fresh, sea and diluted sea water.

MATERIALS AND METHODS

Adult *Talitrus saltator* Montagu (Crustacea Amphipoda) were collected on a Tyrrhenian shore where the seaward theoretical flight direction (STFD) is 264° and the landward theoretical flight direction (LTFD) is 84°. They were kept under natural light in the laboratory in transparent containers lined on the bottom with sand from their home beach. Each specimen was tested once within 7 days of capture. Testing took place under a clear sky and steady sunlight on the tower of the Institute of Zoology in Florence, using a slightly modified version of the methods described in PARDI & PAPI (1953). The animals were placed in a glass ball supported by a plate of glass marked off into sectors with 0 pointing North and surrounded by a screen of translucent plexiglas 5 cm high which hid the immediate surroundings from view. The globe was filled with 500 cm³ of water for each of the tests which were made with: water from the home sea kept no longer than 7 days in the laboratory (total salinity 20‰, dissolved oxygen at the time of testing 9 mg/litre), de-ionized water (dissolved oxygen 10 mg/litre), and sea water diluted with de-ionized water to a salinity of 10, 7, 5 and 3.5‰.

After removing any sand particles clinging to them, 15-20 animals were placed in the water-filled ball and photographed 15 min later by a camera placed under the globe. This was the ideal time lapse as the amphipods did not orient at all during the first few minutes and showed signs of suffering, and occasionally died, after more than 30 min in the water. The photograph provided a reading within 1° of the position of each specimen with respect to North. Animals found floating on their sides, oriented tangentially, and those at the centre and the bottom of the ball, were excluded from the statistical analysis. As a result the number (n) for each position distribution (one position per specimen) varies from 5 to 20. Two tests made at the same time with the same medium were sometimes accumulated, after testing their homogeneity with the *runs test* (BATSCHLET, 1965, pp. 36-37). The resultant vector a and size r of each distribution was calculated (PARDI & PAPI, 1953). Knowing both the STFD (264°) and LTFD (84°), the V test (BATSCHLET, 1972, pp. 63-66) was used to define the concentration of animals in one of the two directions. Two tests made at the same time with different media (sea and de-ionized water) were compared non-parametrically using the Watson U^2 test (BATSCHLET, 1965, p. 35; 1972, p. 84).

RESULTS

Solar orientation in fresh and sea water at various hours of the day. Tests were made at 9.00, 12.00 and 15.00 o'clock (Fig. 1), testing two lots of animals at the same time in identical glass balls filled, respectively, with sea and de ionized water. A series of tests was made in April and again in May, accumulating the distributions obtained from the 2 days of testing under each condition, when the *runs test* showed this to be homogeneous. The resultant direction, length r and value of u (V test) with the level of probability reached are shown for each distribution. Also given are the values of U^2 obtained from a comparison between tests made at the same time with different media (sea and de-ionized water), with the level of probability reached.

As in other populations of *Talitrus saltator* (PARDI & PAPI, 1953; TERRACINI-DE BENEDETTI, 1963), these specimens fled towards land when immersed in sea water and towards the sea when placed in fresh water. The oscillations visible in the diagrams are probably due to phototaxis, particularly marked in fresh water tests at midday where the animals tend to orient towards the sun rather than towards the sea. A comparison between simultaneous tests in sea and fresh water shows that the specimens assume a statistically different direction in the two media in the morning and afternoon while at midday their orientations are not statistically significant, probably due to the positive phototactic tendency of the animals in these experimental conditions (Fig. 1).

Solar orientation in diluted sea water. The results of six tests made on successive days at the same time are shown in Fig. 2 which compares the distribution obtained in water with the same salinity as that of the

ORIENTATION OF *TALITRUS* IN WATER

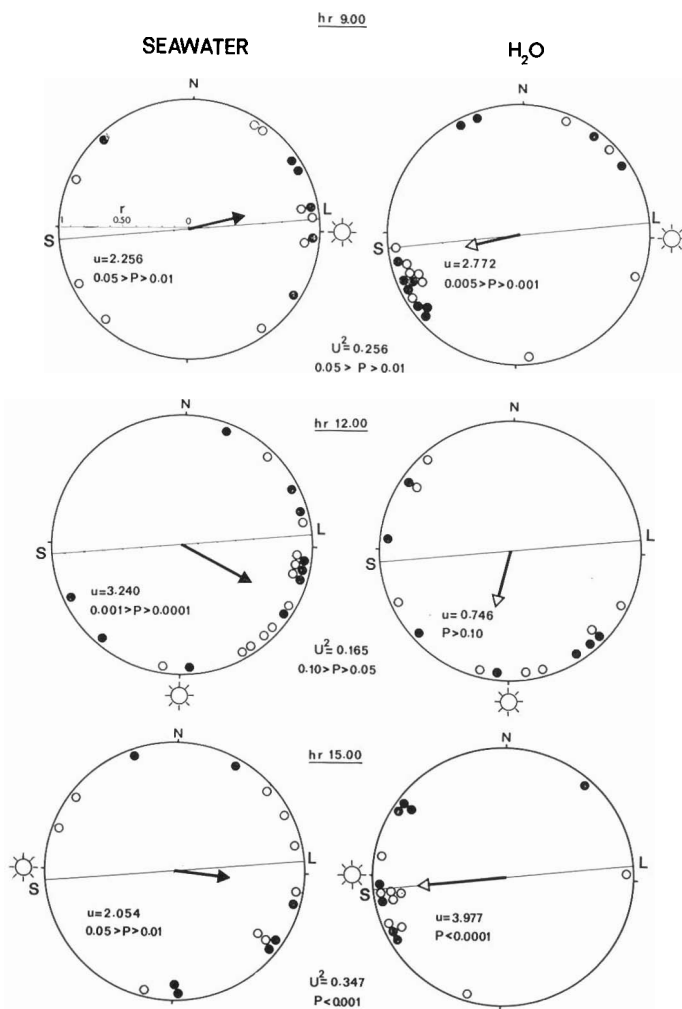


Fig. 1. — Tests on solar orientation in sea (left) and fresh (right) water at 9.00 (top), 12.00 (centre) and 15.00 hr (bottom). Black circles, positions of the animals in April; white circles, positions of the animals in May. Black arrows, animals predominantly oriented landwards; white arrows, animals predominantly oriented seawards. Also shown are the resultant directions and their length r with the radius of the circle corresponding to $r = 1$, the values of u (V test) with the level of probability and the values of U^2 (Watson test) with the level of probability for the comparison between simultaneous tests. S-L, sea-land axis; solar symbol, mean position of the sun.

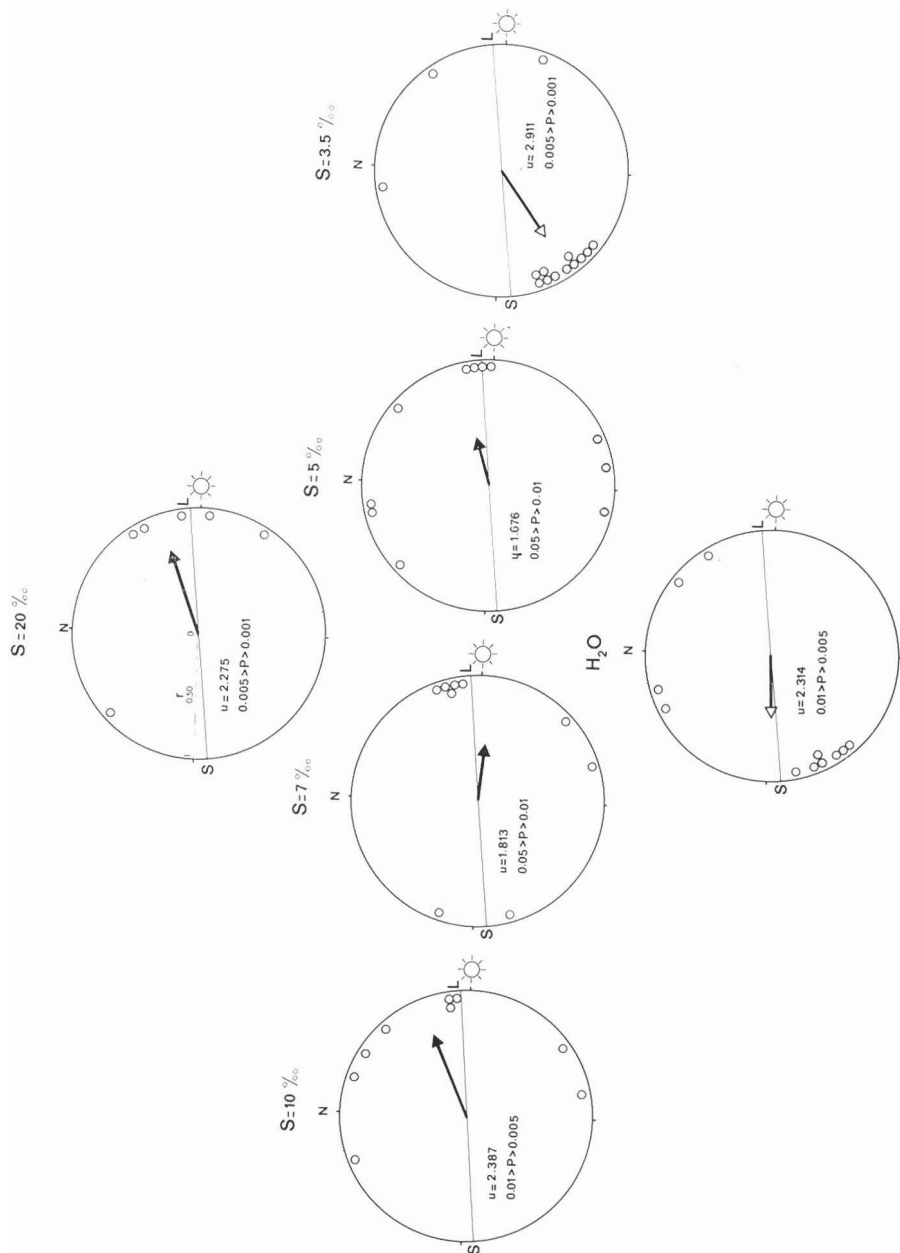


Fig. 2. — Tests on solar orientation in diluted sea water. S , the salinity of the medium which ranged from sea water (top) to fresh water (bottom). Shown in the centre row are the four dilutions tested. Circles, positions of the animals; black and white arrows, animals oriented predominantly landward and seaward, respectively. See Fig. 1 for further explanation.

home sea ($S = 20\text{‰}$), in de-ionized water ($S = 0$) and in sea water diluted with de-ionized water to a salinity of 10, 7, 5 and 3.5‰. The resultant vectors, length r and values of u with the level of probability reached are shown for each distribution.

In saline concentrations of 10, 7 and 5‰ the animals oriented towards land as they did in pure sea water, while a salinity of 3.5‰ causes essentially the same response as de-ionized water. At each increased dilution of the sea water the concentration of the individual distributions diminishes (progressive decrease of r : $S = 20\text{‰}$, $r = 0.677$; $S = 10\text{‰}$, $r = 0.595$; $S = 7\text{‰}$, $r = 0.434$; $S = 5\text{‰}$, $r = 0.364$) together with the value of u which, however, remains above a critical level with a probability of $P = 0.05$ (Fig. 2).

CONCLUSIONS

The amphipod *Talitrus saltator*, from a Tyrrhenian shore population, tends to orient in the direction of land when immersed in sea water and towards the sea when immersed in fresh water (in agreement with TERRACINI-DE BENEDETTI, 1963). This opposing directional tendency is very apparent in the morning and afternoon tests, giving way at midday to a sun-directed orientation caused by the interference of a positive phototaxis. The tendency to orient towards land remains in sea water diluted to a salinity of 5‰, while at a salinity of 3.5‰ the trend reverses towards the sea. Thus the direction of the response depends on salinity. An inversion of the sign in photo-, geo- or rheotaxis according to salinity has been reported and analyzed in marine invertebrates (CREUTZBERG, 1975), often relating this to habitat maintenance and/or horizontally or vertically oriented migrations. These amphipods, instead, do not simply invert tactic sign but rather commutate in photomenotaxis between two supplementary cycles of angular variation.

The biological significance of these responses to saline dilutions and fresh water could be that of facilitating the location and maintenance of the selected habitat, the damp sand at the water's edge. While their oriented return towards land is obviously essential for their survival if carried out to sea by waves or if caught in the frequent large salt water pools or runnels on the beach, the importance in nature of the opposite behaviour is less certain. As *Talitrus* is known to migrate considerable distances on the upper beach (GEPPETTI & TONGIORGI, 1967), they could possibly encounter fresh water streams or pools. After heavy rains, during which the amphipods disperse over the upper beach, the large amount of fresh water in the sand (despite the high humidity of the substratum) could be sufficient to motivate their return seawards.

SUMMARY

Talitrus saltator Montagu (Crustacea Amphipoda) from a Tyrrhenian shore population (STFD = 264°), responded to immersion in sea and fresh water at various hours of the day by orienting, respectively, towards land and towards the sea. The latter response is identical to that obtained on a dry substratum in dehydrated conditions. The landward response remained in dilutions of sea water until a salinity between 5 and 3.5‰ was reached. The biological significance of these responses are discussed.

RIASSUNTO

Sono stati compiuti saggi di orientamento solare con una popolazione tirrenica di *Talitrus saltator* Montagu (Crustacea Amphipoda) (DTFM = 264°) immersi in acqua deionizzata ed in acqua di mare a varie ore del giorno. Gli animali immersi in acqua di mare hanno una direzione di fuga verso terra, mentre si orientano verso il mare se immersi in acqua dolce, come se fossero in ambiente aereo e su substrato asciutto. Diluendo progressivamente l'acqua di mare, si osserva che la risposta orientata verso terra permane fino ad una salinità compresa fra 5 e 3,5‰. Si discute il significato biologico di queste reazioni.

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